

THE PECULIAR LEAF TRICHOMES OF *PETREA VOLUBILIS* (VERBENACEAE)

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ABSTRACT

The structure of the unicellular, heavily silicified leaf trichomes of *P. volubilis* which account for the leaves' "sand paper" structure is clarified: the hairs consist of a disc-like base (in mature leaves frequently located in a shallow depression of the epidermis, and therefore usually not easily recognisable) and a conical, sharp tip in its centre (considered to be the whole hair by earlier workers). The development of these hairs is described, and observations are included about distribution and structure of the other types of non-glandular and glandular trichomes on the leaf blades of *P. volubilis*.

UITTREKSEL

DIE BESONDERSE BLAARTRIGONE VAN *PETREA VOLUBILIS* (VERBENACEAE)

Die struktuur van die eensellige, erg gesilisifieerde blaartrigone van *P. volubilis* wat die "skuurpapier" tekstuur van die blaar verklaar, word verduidelik: die hare het 'n skyfagtige basis (in volwasse blare dikwels in vlak holtes van die epidermis geleë en dus nie maklik uitkenbaar nie) en 'n koniese skerp punt in die middel (deur vorige werkers as die volledige haar beskou). Die ontwikkeling van hierdie hare word beskryf en waarnemings aangaande die verspreiding en struktuur van die ander tipes nie-klier- en kliertrigone op die blaarskyf van *P. volubilis* word ingesluit.

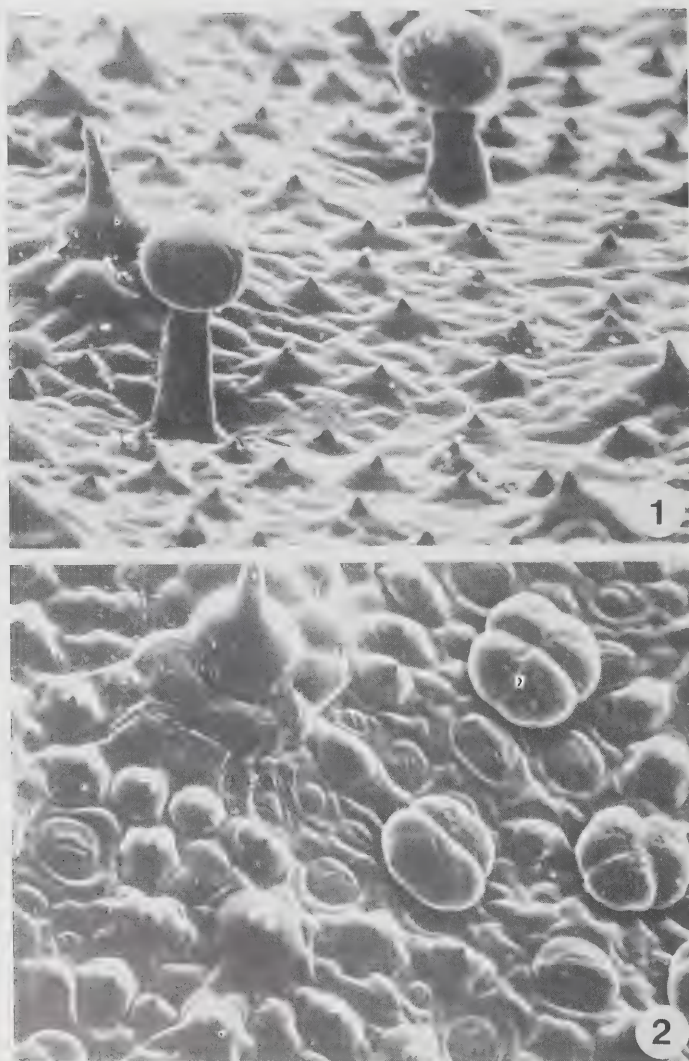
INTRODUCTION

Petrea volubilis L.¹, an attractive twining shrub indigenous to Central America and the West Indies and frequently grown in (sub)tropical gardens of the New and Old World, has evergreen, leathery leaves which are rough to the touch on both surfaces (they feel like sand paper if rubbed between two fingers). This roughness is due to the presence of peculiar hairs, about whose structure there exists a number of quite diverse and controversial interpretations:

Vesque (1885) writes about "peculiar conical *outgrowths* of the outer epidermal wall which are completely silicified". Solereder (1899) observed (in addition to glandular hairs which are not specific to *Petrea*, but characteristic for most Verbenaceae) "short, conical, silicified trichomes which are *embedded singly in the thickened outer wall* of the epidermis cells" and supports his description with

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¹ The spelling *Petraea* often found in horticultural books and journals is inaccurate; so is the frequently used author name Jacquin (Moldenke, 1938: 32).



FIGS 1 and 2.

Scanning electron micrographs of leaf blades of immature leaves. Fig. 1: adaxial surface, Fig. 2: abaxial surface. Figs 1 and 2: $\times 260$. Explanations in the text.

the drawing of raindrop-shaped hairs sunk in the epidermis wall. Metcalfe and Chalk (1950), without further comments, accept his diagnosis. Inamdar's (1969) description and drawing differ considerably from those of the earlier workers: according to him the trichomes are silicified, conical and unicellular (although he pictures a peculiar *three-tipped* hair with a number of "cavities" in the siliceous deposits), and are positioned *on top of* the epidermis, the base of each hair covering the area of numerous epidermal cells. Inamdar (*l.c.*), however, makes no reference to the conflicting results of the previous workers. Also Napp-Zinn (1973) fails to discuss these discrepancies, so that up to now the exact structure of these hairs is still unclear.

It, therefore, appeared worthwhile to re-examine in detail these trichomes, which apparently are specific to *P. volubilis* (and probably *Teijsmanniodendron* according to Metcalfe and Chalk, 1950) and unique in the Verbenaceae—a family characterised by a wide range of different hair forms (cf. Briquet, 1897; Solereder, 1899; Metcalfe and Chalk, 1950).

MATERIAL AND METHODS

Leaf material (usually 5 immature and 5 mature leaves) of *P. volubilis* growing in the gardens in and around Pietermaritzburg was collected and then immediately investigated under the light microscope (transverse sections by hand and epidermis peels) to ensure that the trichomes in question are a stable, always present feature of the species.

SEM investigations: Fresh leaf segments were coated with gold-palladium and viewed with a Hitachi SSM 2 at an accelerating voltage of 10 kV. It was not necessary to use the critical point drying method: no differences whatsoever were observed when pictures of fresh and critical point dried leaves were compared.

TEM investigations: The material was fixed for 2 h in 3% glutaraldehyde followed by 1 h in 1.0% OsO_4 , both in 0.1 phosphate buffer (pH 7.0). After dehydration with graded ethanol the material was embedded in Epon 812. Ultrathin sections were post-stained with uranyl acetate and lead citrate. The electron micrographs were obtained with a Hitachi HU 11.

OBSERVATIONS

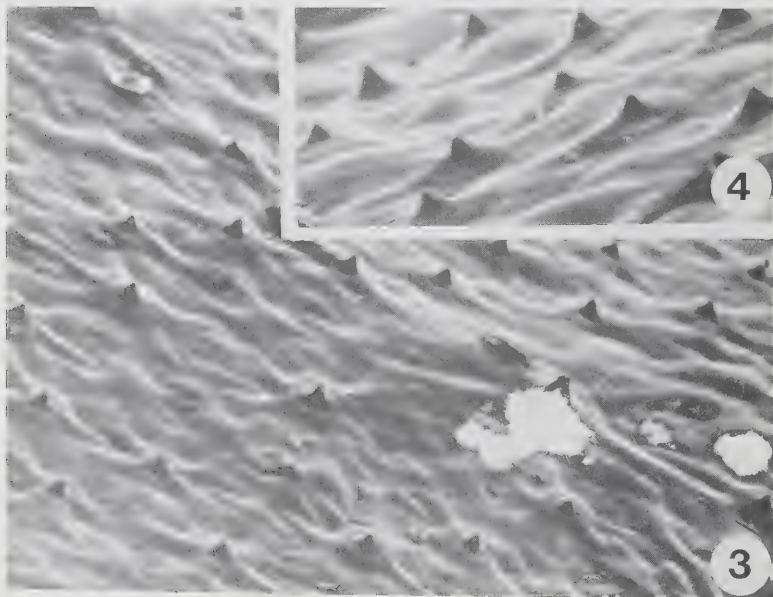
The following types of trichomes are found on the leaf blades of *P. volubilis*: (1) glandular hairs with a (A) short (one-celled) or (B) long stalk and a capitate gland consisting of two to several (6 to 9) radially arranged secretory cells (Figs 1 and 2), and (2) non-glandular trichomes in the form of (A) $\pm$ long, unicellular hairs surrounded by a conspicuous "ring" of cells at the base (Fig. 2) and (B) "short, conical, unicellular hairs" (Solereder, *l.c.*) specific to the species. The occurrence of the various hair types is different on the ad- and abaxial surface of the blades, and also depends on the age of the leaf (Moldenke, 1938, already

mentions that the blades of mature leaves are very rough to the touch on both surfaces, whereas those of very immature ones are less conspicuously so).

The long-stalked glandular hairs are only found on the adaxial surface of very immature leaves, where they may occur in large numbers (and much more closely spaced than in the leaf portion shown in Fig. 1). They seem to completely vanish in old material (due to breaking or falling off?).

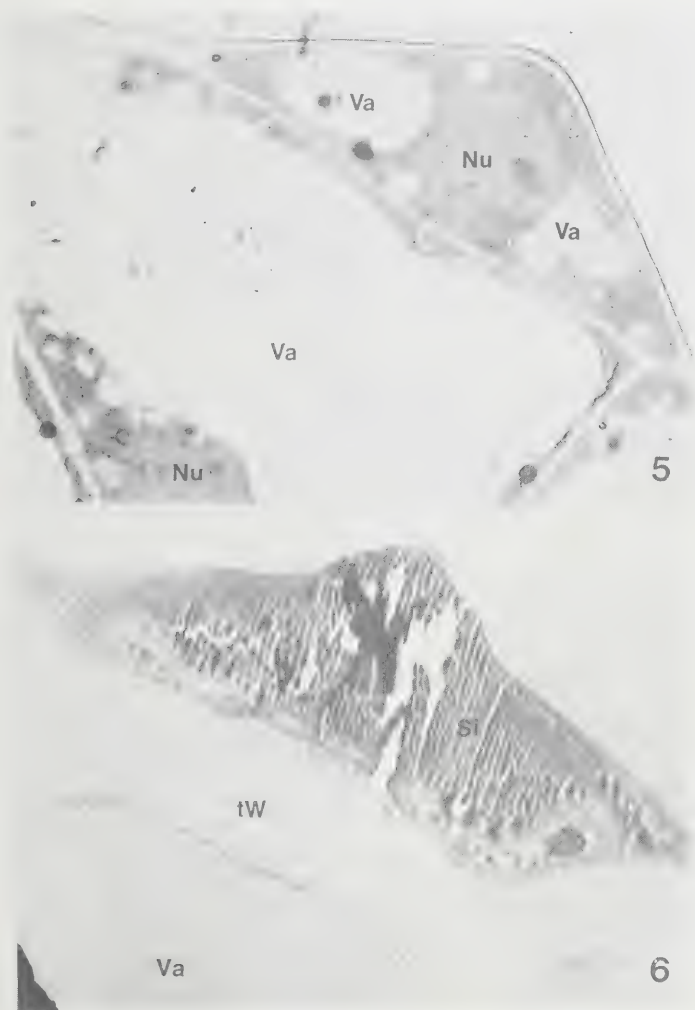
The short-stalked glands are very common on the abaxial surface of young and old leaves, but are often absent from the adaxial surface (if present, they never occur in large numbers and are sunk in crypts; their appearance is similar to that of sunken glandular hairs of *Avicennia marina*: Fahn and Shimony, 1977: Plate 1C). In mature leaves the number of secretory cells per gland is (6)8(9), in young and very young leaves it appears to be less (2-6; even recognisable in Fig. 2: the depressions on the glands correspond with the walls between two secretory cells). Obviously the fewer celled glandular trichomes represent younger stages of development (cf. Fahn and Shimony, 1977: Fig. 2J-N).

The very sparse, long, unicellular hairs (Figs 1 and 2) are found on the abaxial surface (particularly in young material) and (very seldom) on the upper epidermis, where they seem to completely disappear in mature leaves.



FIGS 3 and 4.

Scanning electron micrographs of adaxial surface of mature leaves. Fig. 3: $\times 260$ Fig. 4: $\times 400$. Explanations in the text.



FIGS 5 and 6.

Transmission electron micrographs of unicellular hairs. Fig. 5: off-median section of young, not yet silicified hairs (immature leaf). Fig. 6: close-to-median section of fully developed, heavily silicified hair (mature leaf); silicifications partially broken out. Nu: nucleus, Si: siliceous deposits, tW: thickened, layered cell wall, Va: vacuole. Figs 5 and 6: $\times 4200$.

The "short, conical hairs" sensu Solereder (*l.c.*) are densely distributed on both surfaces, although usually in much greater abundance on the adaxial surface (compare Figs 1 and 2). Although already present in immature leaves (Figs 1 and 2) they become particularly conspicuous on the adaxial surface of mature leaves (Figs 3 and 4), where they, in fact, look like Vesque's (*l.c.*) "peculiar outgrowths of the epidermis". Contrary to Solereder's (*l.c.*) interpretation, however, they are not raindrop-shaped and embedded in the outer epidermal wall: longitudinal sections prove that they actually sit singly on top of cells and, strictly speaking, are not conical, but consist of a flat, more or less disc-like base with a conical tip in its center, both of which are, in the mature stage, heavily silicified (Fig. 6). Solereder (*l.c.*) considered these tips, which are responsible for the "sand paper texture" of the plant's leaves, to be the whole hairs.

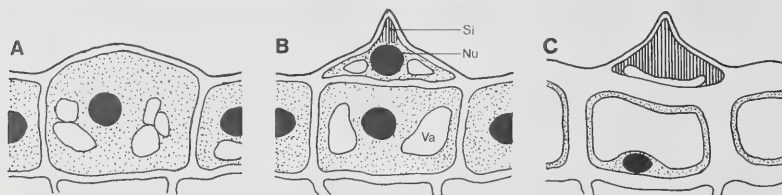


FIG. 7.

Schematic representation of three stages of development of the peculiar, unicellular trichomes. A: enlarged epidermis cell (hair initial), B: young hair with starting silicification, C: mature, heavily silicified hair. Nu: nucleus, Si: siliceous deposits, Va: vacuole. Further explanations in the text.

The development of these trichomes is as follows (Fig. 7): at an early stage of development of the leaf an epidermis cell increases in size and extends above the surrounding epidermal cells (Fig. 7A). This hair initially shows no significant differences from the neighbouring cells (cytoplasm dense, occupying almost the whole cell lumen; few, small vacuoles; large nucleus). After a periclinal and somewhat unequal division, hair cell and basal cell originate. The basal cell is usually larger than the hair cell and is generally not distinguishable from the neighbouring epidermis cells (Fig. 7B). The protoplast of the basal cell soon forms a layer against the cell wall so that a large central vacuole originates, while the cytoplasm still occupies most of the cell lumen of the hair cell (Fig. 5). It is presumed that, at this stage at the latest, the silicification of the conical tips of the hairs begins, although there is no concrete evidence for this (median sections of this stage of development always ripped out in the region of the tips indicating that it was already filled with difficult-to-cut siliceous deposits). As development continues the walls of the basal cells and the neighbouring epidermis cells thicken rapidly (the outer epidermal walls more than the inner ones) and become conspicuously layered (Fig. 6), and the hairs (whose walls do not thicken to that extent) become almost completely filled with siliceous deposits (Figs 6 and 7C).

At this stage (i.e. in mature leaves), the outer epidermal walls have become quite uneven, and the disc-like bases of the hairs often are somewhat obscured, since they are no longer—as in immature leaves—clearly raised above the level of the outer epidermal walls of the surrounding cells (compare Figs 1, 2 and 3, 4 and 6).

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